PLATE IV.

Fig. 9. Section of the free edges of two lamellæ of the lung-book.
10. Section through lamellæ of lung-book near their base.
11. Part of the wall of the air-space towards the centre.
12. Section of wall of air-space towards the side.
13. Side view of mouth and surrounding parts. The left first and second appendages have been removed and the thorax laid open. i. and ii., right first and second appendages; *car.*, carapace; *eps.*, epistome; *m.*, mouth; *p.s.t.*, sense-organ on base of appendage ii.
14. Ventral sclerites of second and third free segments, viewed from inside.
15. Section of wall of stercoral pocket.
16. Section of one of the Malpighian tubes.
17. Section of epithelium of proctodæum.

PLATE V.

Fig. 18. Ventral surface of abdomen of *Phrynus reniformis*, with egg-sac.
19. Young embryo of *Phrynus reniformis*: surface view.
20. Side view of embryo of *Phrynus annulatipes*, ×9. *l.o.*, lateral organ.
21. Schematic longitudinal vertical section of *Phrynus annulatipes*, ×. *o.e.*, median eye; *gen.a.*, genital aperture; *Sto.*, stercoral pocket; *Pr.*, proctodæum.
22. Longitudinal section of first four abdominal segments. ×.
23. Longitudinal section through front part of coxal gland and duct.

On the Aortic-Arch System of *Saccobranchus fossilis*.

By R. H. BURNE, B.A. Oxon., Assistant in Museum, Royal College of Surgeons, London. (Communicated by Prof. G. B. HOWES, F.L.S.)

[Read 5th April, 1894.]

IN tropical countries, but more especially in India, where the streams and tanks are liable to become dry in the hot season, a number of the freshwater fishes have acquired the power of living for a longer or shorter time out of water, and are thus enabled either to migrate to places where water is more abundant, or to bury themselves deep down in the mud to await the revivifying rains. Many years ago * reports that fish were often dug up in spots that had been dry for months, or were found

* For the early literature of this subject see Boake, Journ. Ceylon Branch Asiat. Soc. 1865, and Day, Proc. Zool. Soc. 1868, p. 274.

wandering far from any water, stirred the curiosity of naturalists, and finally led to the recognition, as accessory respiratory organs, of certain structural modifications occurring in these fishes.

For some time the exact method by which this respiration was effected remained doubtful. However, during the last twenty-five or thirty years numerous interesting experiments have been performed by Day and others * upon most of these Indian freshwater fishes, which tend to prove that the modifications in the pharyngeal region of these creatures (epibranchial and other organs) do not contain water for moistening the gills as was originally supposed, but air for purposes of direct aerial respiration †. In certain other air-breathing fishes, *i. e.* the bony Ganoids and the Dipnoi, the same end is attained by a modification of the swim-bladder.

Further details upon this subject are unnecessary, as my object is merely to draw attention to the fact that among fishes bearing no close relationship to each other there are to be found specialized organs differing in their morphological characters, but which are all, physiologically speaking, lungs.

In the East-Indian rivers there is to be found a curious air-breathing Siluroid, by name *Saccobranchus*, in which the accessory respiratory organ takes the form of a pair of long narrow air-pouches, which lie along the back on either side of the vertebral column above the transverse processes, and extend for three parts the length of the fish, from the branchial chamber to within four inches of the tail. Venous blood is conveyed directly from the heart to the air-sacs by branches of a pair of the afferent branchial arteries, and returned, after oxygenation, into the aorta.

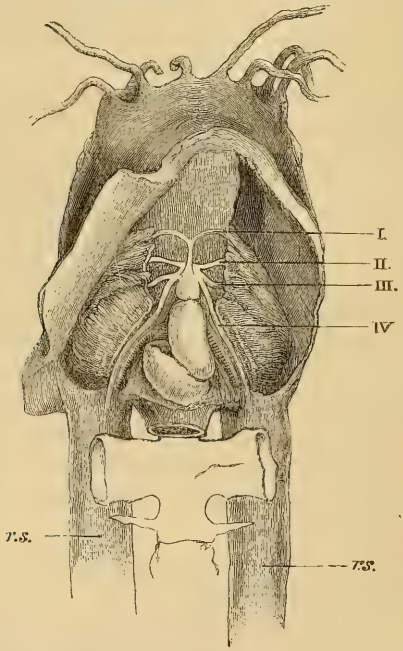
Hyrtl ‡, who has worked out the anatomy of this fish, describes the arrangement of the branchial arteries with reference to the air-sacs as follows :—"The fourth left branchial artery surpasses

* Day, Proc. Zool. Soc. 1868, p. 274, and Journ. Linn. Soc. (Zool.) vol. xiii. p. 198; Dobson, Proc. Zool. Soc. 1874, p. 312.

† From his researches on the blood-supply to the supra-branchial chamber in the Ophiocephalidæ, Hyrtl considers that this organ is not for breathing air, but is probably a water-reservoir for moistening the gills. (Hyrtl, "Ueber das Labyrinth und die Aortenbogen der Gattung *Ophiocephalus*," Sitz. Akad. Wiss. Bd. x. 1853, p. 148.)

‡ Hyrtl, "Zur Anatomie von *Saccobranchus singio*," Sitz. Akad. Wiss. 1853, Bd. xi. Heft 1, p. 302.

all the others on the same side in magnitude. The right, on the contrary, is smaller than all preceding it on its side. The left fourth branchial artery leaves the fourth gill-arch to pass to the ventral wall of the dorsal respiratory sac, on which it passes to the hinder end of the sac, giving off alternating side-twigs. On the right, the artery passing to the respiratory sac is not a prolongation of the fourth, but of the first branchial artery, and runs not on the ventral, but on the dorsal wall of the sac." This statement of Hyrtl's is endorsed by Hubrecht*, who dissected one of these fishes at the request of Day when the latter was working at the physiology of this apparatus.



Branchial region (nat. size) of *Saccobranchus fossilis*, showing the arrangement of the branchial arteries, seen from the ventral aspect.—I, II, III, IV, branchial arteries; *r.s.*, respiratory sacs.

In a specimen of *Saccobranchus fossilis* in the Museum of the Royal College of Surgeons (No. 1061 G), which I dissected last year, the branchial arteries do not answer to this description, for here the arteries are quite symmetrical on either side. The

* Day, Journ. Linn. Soc. (Zool.) vol. xiii. p. 198.

fourth on both sides is considerably larger than the others, and, after coursing along the fourth gill-arch, is continued upon the ventral wall of its respective air-sac. The first, second, and third go to their several gills in the ordinary way. The first on the right does not differ in size from its companion on the left, and rapidly diminishes in calibre in its course along the gill, so that I was unable to trace it more than half an inch or so.

Unfortunately it was not possible to inject this fish; but the vessels were sufficiently conspicuous to leave no doubt in my mind as to the accuracy of this observation.

It is to be observed that Hyrtl made his observations upon *Saccobranchus singio*, so that it is possible that this distribution of the branchial vessels may have a specific significance, and not be merely a case of individual variation.

With reference to this arrangement of the aortic arches in *Saccobranchus*, it is interesting to briefly review the work that has already been done in connection with the blood-supply to organs of aerial respiration in fishes and the higher Vertebrata.

Beginning at the top of the scale and working downwards, we find that a general law has been laid down by Boas* to the effect that in the Amphibia and all higher Vertebrata the pulmonary artery is always derived from the fourth branchial aortic arch†.

This generalization is considerably strengthened by van Bemmeln's‡ discovery in embryonic Reptilia and Aves of two gill-clefts and an aortic arch lying between the systemic and pulmonary arteries; and still further by Zimmermann's§ demonstration of an aortic arch in the same position in embryos of the rabbit and Man.

Coming now to the Dipnoi, amphibious fishes whose swim-bladder has been modified for purposes of aerial respiration, matters become complicated by the reduction and compression of the branchial apparatus. It is possible, however, in *Ceratodus*,

* Boas, Morph. Jahrb. Bd. vii. 1882, p. 488, "Ueber den Conus Arteriosus und die Arterienbogen der Amphibien;" and Morph. Jahrb. Bd. xiii. 1887–88, p. 115, "Ueber die Arterienbogen der Wirbelthiere."

† That is, the 6th visceral aortic arch. For simplicity's sake I count from the 1st branchial aortic arch.

‡ Van Bemmeln, "Die Visceraltaschen und Aortenbogen bei Reptilien und Vögeln," Zool. Anzeig. 1886, pp. 528 & 543.

§ Zimmermann, "Ueber einen zwischen Aorten- und Pulmonatbogen gelegenen Kiemenarterienbogen beim Kaninchen," Anatomisch. Anzeig. 1889, p. 720.

the member of the family least modified in this respect, to make out that the swim-bladder is supplied from the fourth aortic arch*. In *Protopterus* † this is no longer possible, as the efferent branchial vessels have become fused on either side into a common trunk, from the posterior face of which the pulmonary artery arises. The branchial compression is still more advanced in *Lepidosiren* ‡, the remaining member of the family; so much so indeed, that the pulmonary artery apparently takes its origin from the third aortic arch. Whether this is really the case I must leave an open question, although the great resemblance between the aortic arches in this fish and in some of the lower Amphibia § would incline one to think not.

In the two Ganoids *Polypterus* and *Amia* ‖ the pulmonary artery takes its origin, according to Boas ¶, as a large branch of the fourth efferent branchial vessel. The main trunk of this vessel, after giving off the pulmonary artery, passes on in a reduced condition, and joins the third efferent branchial vessel. Thus Boas regards the pulmonary artery of these fish as a derivative of the fourth branchial aortic arch alone.

In contradiction to this, it appears, from the figure of the aortic arches of *Amia* given by Ramsay Wright, that the third aortic arch is also involved in the formation of the pulmonary artery. This effect is produced by the connection between the third and fourth efferent branchial vessels being represented as a branch of the third, and not a continuation of the fourth efferent branchial vessel. A very slight alteration in the drawing is enough to accomplish this; for if the connection in question is drawn sloping from the third branchial vessel towards the middle line, it appears to be part of the third arch; if away from the middle line ever so slightly, it would be called a continuation of the fourth arch.

* Boas, Morph. Jahrb. Bd. vi. 1880, p. 321, "Ueber Herz und Arterienbogen bei *Ceratodus* und *Protopterus*."

† Parker (W. N.), "On the Anatomy and Physiology of *Protopterus annectens*," Trans. Roy. Irish Acad. vol. xxx., in which paper other references will also be found.

‡ Hyrtl, *Lepidosiren paradoxa*, and Bischoff, "Sur le *Lepidosiren paradoxa*," Ann. Sci. Nat. (Zool.) vol. xiv. 1840, p. 116.

§ Bischoff, *l. c.*

‖ Johannes Müller, "Beiträge zu Bau und Grenzen der Ganoiden," Abhandl. Akad. Wiss. Berlin, 1844, p. 117; Boas, Morph. Jahrb. Bd. vi. p. 321.

¶ Boas, Morph. Jahrb. Bd. vi. pp. 342 & 351.

Having regard to the fact that Ramsay Wright's figure is a diagram in the Introduction to a General Natural History of Fishes' *, but that Boas, on the other hand, was working specially upon the aortic arches of these Ganoids, it seems to me that we are justified in electing to follow Boas in this matter, and, with him, to look upon the pulmonary artery of *Polypterus* and *Amia* as a derivative of the fourth aortic arch alone †.

Finally, we come to the mixed group of tropical freshwater fishes in which a modification of the pharyngeal region does duty as a lung. The anatomy of the epibranchial organ of the Labyrinthici has been worked out by Zograff ‡; and as regards the blood-supply to that structure, he succeeded, after several disappointments, in proving that the blood is brought to the epibranchial organ by the fourth aortic arch.

The suprabranchial chamber of the Ophiocephalidæ, which so much resembles that of the Labyrinthici, according to Hyrtl does not receive its blood from the heart, although the fourth branchial artery passes through it. From the subsequent experiments that have been performed on these fishes, it is very probable that Hyrtl was mistaken, and that these chambers are organs for the respiration of air. In this connection it is well to remember that Zograff found great difficulty in injecting the blood-vessels to the epibranchial organ in the Labyrinthici.

Now, as to *Saccobranchus*, we have seen that Hyrtl and Hubrecht found that the blood was carried to the respiratory sacs by the first aortic arch on one side, and the fourth on the other. In my specimen, on the contrary, it was supplied by the fourth on both sides.

The peculiar spirally-coiled epibranchial organ of *Heterotis Ehrenbergii*, one of the Osteoglossidæ §, receives its blood from the fourth aortic arch, as also does that of *Chanos salmonæus* (*Lutodeira chanos* of Hyrtl) ‖. In the Cuchia eel, *Amphipnous*

* Ramsay Wright, 'Standard Natural History,' vol. iii. p. 48.

† Boas, Morph. Jahrb. Bd. vi. pp. 342 & 351.

‡ Zograff, Quart. Journ. Micros. Sci. vol. xxviii. 1888, p. 501, "On the Construction and Purpose of the so-called Labyrinthine Apparatus of the Labyrinthic Fishes."

§ Hyrtl, Denkschr. Akad. Wiss. Bd. viii. 1854, p. 73, "Beitrag zur Anatomie von *Heterotis Ehrenbergii*."

‖ Hyrtl, "Ueber das Epigonale Kiemenorgan von *Lutodeira chanos*," Denkschr. Akad. Wiss. Bd. xxi. 1863, p. 1.

cuchia *, the two respiratory bladders on either side of the neck obtain their blood-supply from the first pair of branchial aortic arches.

In looking through the above list, one is at once struck by the frequency with which the pulmonary artery is derived from the fourth aortic arch; and this not only when the lungs are in all probability homologous structures, but in creatures having different kinds of air-breathing organs, some of which can bear no morphological relationship to each other.

There certainly are exceptions, but they are comparatively very few; in fact, even including *Lepidosiren*, which, from the compressed condition of its branchial apparatus, ought scarcely to be used as an argument either way, they only amount to three; and even of these three we have seen that one, i. e. *Saccobranchus*, is sometimes found in what may be called the normal condition.

The general tendency appears to be that any organs modified to act as lungs, no matter what may be their morphological characters, are supplied with blood by the fourth branchial aortic arch. In the higher Vertebrata this is the case without exception; and even among fishes, where presumably the organ specialized for breathing air is not so firmly established, this is still the case, although liable to variation.

Saccobranchus and *Amphipnous* agree in respect to the origin of their afferent pulmonary vessel from the afferent branchial system; and therefore it is specially interesting to note that *S. singio* is abnormal in the partial realization of that character (origin of pulmonary artery from the first branchial arch) which is diagnostic of *Amphipnous*.

It has been suggested to me by my friend and late teacher Prof. Howes, that the variations occurring in the pulmonary artery of these fishes may find a parallel in the variability which he observed in the first appearances of the epiglottis in the Amphibia †. So far as I am aware, this may very well be the case, since there appears to be considerable liability to variation in organs that are in the initial stages of their development, and, so to speak, still on their trial.

* Hyrtl, "Ueber den Amphibienkreislauf von *Amphipnous* und *Monopterus*," Denkschr. Akad. Wiss. Bd. xiv. 1857, p. 39.

† G. B. Howes, "On a hitherto unrecognized Feature in the Larynx of the Anurous Amphibia," P. Z. S. 1887, p. 491.

I cannot conclude without tendering my warmest thanks to Prof. Howes for the trouble he has taken in helping me with this paper, and for many kindly suggestions and corrections.

Note (25 *Sept.*, 1894).—Since writing the above, my attention has been called to two short papers by Jobert on the aerial respiration of certain fishes of the Amazon (Ann. Sci. Nat. sér. 6, vol. v. art. 8, & vol. vii. art. 5). In three instances (*Callichthys*, *Hypostomos*, and *Doras*) aerial respiration is effected by means of a peculiarly modified portion of the intestine which receives its blood-supply from the aorta; the blood, however, is partly venous, as the afferent and efferent branchial vessels are continuous and allow the blood to pass directly from one to the other. In the case of two other fishes (*Erythrinus* and *Sudis*) the swim-bladder functions as a lung, receiving venous blood from the mesenteric veins, and also arterial blood from the aorta. It will be noticed that all these fishes, as regards their pulmonary blood-supply, are exceptions to the general tendency indicated above: that this should be so, especially in the case of the intestinal breathers, is not a matter for surprise; here, if anywhere, one would expect to find variation, for the distance of the modified organ from the pharynx suggests the probability that the blood-supply to the newly acquired lung might be procured from some already existing neighbouring vessel, rather than directly from the distant aortic arch.—*R. H. B.*